

Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII

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Received September 2, 1992

BERG, B., McCLAUGHERTY, C., and JOHANSSON, M.-B. 1993. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII. *Can. J. Bot.* **71**: 680–692.

The patterns of some chemical changes and litter mass-loss rates were investigated for a variety of types of decomposing litter in pine forests under different climatic conditions and at sites with different nutrient status. A mixed deciduous forest was also compared. In initially chemically identical Scots pine needle litter incubated under different climatic conditions, the lignin concentration increased faster as a function of accumulated mass loss when the climatic conditions promoted a higher initial mass-loss rate. Also under artificially created conditions, e.g., after fertilization and irrigation, the same phenomenon occurred. Litter mass-loss rates decreased during decomposition as lignin concentrations increased. The relative decrease was significantly larger at sites with a climate that promoted an initially higher mass-loss rate. At the same lignin concentration, however, the mass-loss rate was significantly lower in drier and colder conditions, viz. climatic conditions that promote a lower initial mass-loss rate. Nevertheless, at very high lignin concentrations that lignin clearly dominated over climate as a rate-regulating factor. A possible consequence of this observation could be a higher rate of organic matter accumulation at sites that initially promote a high initial mass-loss rate for litter than at sites with conditions that give lower initial rates, at least for a given species of litter.

Key words: litter, decomposition, lignin, chemical changes, climatic transect, effect of climate change.

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Les auteurs ont étudié les patrons de certains changements chimiques et des taux de perte de masse des litières, chez diverses litières en décomposition, dans des forêts de pin venant sous différentes conditions climatiques et sur des sites avec différents statuts nutritifs. Ils ont également comparé une forêt mixte décidue. Chez des litières de pin sylvestre chimiquement identiques au départ et incubées sous différentes conditions climatiques, la teneur en lignine augmente plus rapidement en fonction de la perte cumulée de biomasse, lorsque les conditions climatiques encouragent un taux de perte de biomasse initiale plus élevé. Sous des conditions produites artificiellement, e.g., après fertilisation et irrigation, on observe le même phénomène. Les taux de perte en masse de la litière diminuent au cours de la décomposition, à mesure que les teneurs en lignine augmentent. La diminution relative est significativement plus grande aux sites où le climat provoque un taux de perte de biomasse initiale plus élevé. Avec une même teneur en lignine, cependant, le taux de perte en biomasse est significativement plus faible sous des conditions plus sèches et plus froides, c'est-à-dire des conditions climatiques qui provoquent un taux de perte de biomasse initiale plus élevé. Tout de même, avec de très fortes teneurs en lignine, celles-ci dépassent nettement le climat comme facteur régulateur du taux de décomposition. Une conséquence possible de cette observation pourrait être un taux plus rapide d'accumulation de matière organique aux sites qui provoquent un taux de perte de biomasse initiale plus élevé, qu'aux sites ayant des conditions qui favorisent des taux initiaux plus faibles, au moins pour une espèce de litière donnée.

Mots clés : litière, décomposition, lignine, modifications chimiques, transect climatique, effet des changements climatiques.

[Traduit par la rédaction]

Introduction

When plant litter is shed each litter type can have a different composition of both inorganic nutrients and organic chemical compounds. During the process of decomposition the chemical composition of litter changes; the more easily available compounds are decomposed first and the more resistant compounds become more concentrated (Berg et al. 1982), giving the litter a progressively increasing recalcitrance (McClagherty and Berg 1987). In addition, recalcitrant lignin-like compounds are formed during the decomposition process (e.g., in the form of humic acids) (Stevenson 1987) and many types of decomposing litter

exhibit an increase in the amount of recalcitrant substances that they contain.

Because of their low rate of decay, lignin and lignin-like compounds have long been considered to exert a negative effect on the decomposition rate (Fogel and Cromack 1977). Berg and Staaf (1980) proposed two phases in Scots pine needle litter decomposition: one initial phase regulated by the concentration in the litter of the main nutrients, and a later phase in which decomposition rate was ruled by the mass-loss rate of lignin.

This rate-regulating effect of lignin in a later phase has since then been generalized to some other needle and leaf litters (McClagherty and Berg 1987; Berg and Lundmark 1987).

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Based on the progressively increasing recalcitrance of decomposing litter, Berg and Ågren (1984) estimated a theoretical final mass-loss rate for a given litter type in a given system based on the quality of the litter in a very late stage of decomposition (i.e., in the humus stage). This final rate of decomposition was reached well after the onset of the lignin-regulated phase.

Soil moisture and soil temperature have a strong influence on litter-decomposition rates, and in early stages of decomposition their influence may be estimated (Jansson and Berg 1985). The interaction between rate-regulating factors, such as the content of nutrients and lignin, and other factors, such as soil temperature and moisture, were investigated only to a limited extent by Flanagan and Veum (1974), Meentemeyer (1978), and Meentemeyer and Berg (1986).

The present synthesis paper has two aims. One is to show that the increase in concentration of lignin during litter decomposition varies with the ecosystem where the litter is incubated and with the nutrient status of the litter. The other is to find and establish differences in the rate-regulating pattern of lignin for one litter type incubated under different climatic conditions, which could illustrate effects of climate change.

Site description

Studies were carried out intensively at eight sites (2, 3, 4, 6, 8, 13, M, and B.I.) that are described in detail below. For 10 sites (10, 100–108) at which the studies were less intensive, only the main site characteristics are given in Table 1 and below. The site numbers correspond to those previously given by Berg et al. (1986, 1991a). Further plot and site data are given by the references indicated in Table 1.

All sites except Blackhawk Island (B.I.) had Scots pine (*Pinus silvestris* L.) monocultures. The Malung site (M) also had lodgepole pine (*Pinus contorta* Dougl.) monoculture plots.

The B.I. site was different from the other sites since it was a mixed deciduous forest with a mull soil and with a dominant vegetation of sugar maple (*Acer saccharum* Marsh.) and very little understory. The site was relatively nutrient rich. A further site description is given by Pastor et al. (1982).

Sites 4 and 6 had experimentally modified plots (see Table 1). At the Norrliden site (4), plot 4:29 had been fertilized with 120 kg N (as NH_4NO_3)/(ha · year) since 1971, and since 1974 the annual dosage has been 80 kg. In addition 40 kg of P and 76 kg of K were added in both 1971 and 1976.

The Jädraås site (6) had five plots with Scots pine, of which plot 6:51 was a 130-year-old forest, and plots 6:15, 6:5, 6:4, and 6:17 were in a 30-year-old forest in which the three latter plots were experimentally modified (Table 1). The experimentally modified plots at site 6 (Table 1) were either fertilized with 80 kg N (as NH_4NO_3)/(ha · year) (6:5) or irrigated with about 250 mm water (6:17) during the dry summer months, beginning in 1976. Thus the effective annual precipitation was increased from the average 609 mm to about 860 mm (cf. Berg et al. (1991c)). The understory in these modified stands had changed with respect to the control plot. A closer description is given by Berg et al. (1991c, 1992).

Site 3 (Manjärärv) had three subplots that had different nutrient status and different understory, 3:1 being the most nutrient poor as well as dry and 3:3 being the wettest and most nutrient rich plot.

The size and shape varied among the plots: at site 2 the plot measured 10 × 30 m; at site 4 each plot was 30 × 30 m; at site 6 plot 6:51 measured 100 × 300 m, and all other plots were 30 × 30 m; at site 8 the plot was 40 × 40 m; at site 13 the plot was 20 × 30 m; at site M all plots measured 30 × 30 m, as did the plot at site B.I., and plots 3:1, 3:2, 3:3, 10:1, and sites 100–108.

Additional site information is given in Table 1, as are references to original site descriptions.

Materials and methods

Needle collection, storage, and sample preparation

Litter types and denominations

In this study we used both local litter, collected and incubated at particular sites, and a unified litter preparation of Scots pine needles, collected at a single site and incubated at many sites. Experimental litters were also used. All Scots pine needle litter collected at the main stand at the Jädraås site was called unified litter. All litter collected at the other natural (control) sites and plots is called local litter. Further, all litter collected at fertilized stands and all litter that was transplanted to a site other than its origin is called experimental litter. An exception to this is the unified litter.

Unified and experimental litters

Unified brown needle litter was collected from a single stand at abscission each year (late September) by gently shaking the branches. The stand was 15 years old when the study began in 1973. All trees sampled were located in an area less than a hectare. This litter varied widely in chemical composition over 14 years of collections (Appendix 1).² Green Scots pine needles were collected in the same area and taken during winter as 2- and 3-year-old needles (Berg and Ekbohm 1991). Experimental Scots pine needle litter was collected during litterfall at the experimental plot Lisselbo (LISS), a fertilization optimization study plot (Tamm et al. 1974; Berg and Staaf 1980). The collection and decomposition of these types of needle litters was described earlier by Berg et al. (1987). Lodgepole pine needle litter was sampled at site M:17. This sampling was described by Berg and Ekbohm (1991).

Local litters

Local brown needle litter was collected at sites B.I. and 2, 3, 4, 6, 10:1, 100–108, and sites M:17–19. These samplings took place at time of abscission.

Sample preparation

The sampled litter was air dried and stored dry at room temperature until sample preparation took place. Before weighing, the needles were allowed to equilibrate at room temperature to a constant moisture level, approximately 5–8%. For a given sample the largest difference in moisture was less than ± 0.5% units from the average as determined by 20 or 25 samples.

Experimental design, incubation, and mass-loss determination

At all sites, except B.I., litter samples were incubated in a randomized block design at 25 spots within the plot. The procedures of incubation and sampling of litterbags were very similar among the plots of sites 2–8, 10:1, 13, 100–108, and site M, but more detailed descriptions were previously published (Berg et al. 1991c; Berg and Lundmark 1987; Berg et al. 1982). The design for sites 10:1 and 100–108 was described by Johansson (1986) and for site B.I. by McClaugherty and Berg (1987). At the B.I. site litter samples were located completely randomly along transects within the plot.

Each incubation spot measured about 1 × 1 m. At all sites the samples were placed on the A_{00} layer and incubation time was up to 5 years, with samplings normally 2–3 times a year.

When collected (one sample from each incubation spot) the samples were transported directly to the laboratory and cleaned of mosses, lichens, and other remnants of ingrown plants. After the removal of plant remains, the loss of dry mass of the needles was determined by drying the samples to a constant mass at 85°C (50°C for the B.I. site). Mean values of mass loss were calculated for each sampling ($n = 25$ at all plots except for site B.I. with $n = 4–10$). After this the samples were combined for chemical analysis.

²Basic data on initial chemical composition of the litter types included in this study, as well as data on chemical changes referred to as appendices are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

TABLE 1. Overview of site locations and climatic data (basic data for all these sites are given by Berg et al. 1991a and Pastor et al. 1982)

Site name and No.	Long.	Lat.	Alt. (m)	Mean annual temp. (°C)	Mean annual pptn. (mm)	Soil texture	Ground vegetation type	Ref. ^a
Main sites								
Harads 2	66°08'N	20°53'E	58	+1.3	650	Fine sand	Lichen	1, 8, 9
Manjärvi 3:1	65°47'N	20°37'E	135	+1.0	700	Fine sand	Lichen rich	1, 8, 9
3:2	65°47'N	20°37'E	135	+1.0	700	Silt	Dwarf shrub ^b	1, 8, 9
3:3	65°47'N	20°37'E	135	+1.0	700	Silt	Low herbs	1, 8, 9
Norrleden Control 4:23	64°21'N	20°53'E	260	+1.2	595		Dwarf shrub ^b	1, 3
Fert. 4:29 ^c	64°21'N	20°53'E	260	+1.2	595		Grass (<i>Carex</i>)	1, 3
Jädraås (old forest) 6:51	60°49'N	16°30'E	185	+3.8	609	Fine sand	Dwarf shrub ^b	1, 2
Jädraås (young experimental stand) Control 6:15	60°49'N	16°30'E	185	+3.8	609	Fine sand	Dwarf shrub ^b	1, 2
Fert. 6:5 ^c	60°49'N	16°30'E	185	+3.8	609	Fine sand	No ground vegetation	1, 2
Irrig. 6:17	60°49'N	16°30'E	185	+3.8	609	Fine sand	Dwarf shrub ^b	1, 2
Irrig. + fert. 6:4 ^d	60°49'N	16°30'E	185	+3.8	609	Fine sand	Tall herbs	1, 2
Nennesmo 8	58°16'N	13°35'E	155	+6.2	930		Dwarf shrub ^a	1
Ehrhorn 13	53°00'N	09°57'E	81	+8.7	730		Grass (<i>Carex</i>)	1, 9
Malung M:17	60°33'N	13°44'E	375	+2.8	705	Fine sandy till	Dwarf shrub ^b	4
M:18	60°38'N	13°37'E	400	+2.0	700	Sandy till	Dwarf shrub ^b	4
M:19	60°35'N	13°34'E	435	+1.8	710	Fine sandy till	Dwarf shrub	4
Lisselbo ^e LISS	60°28'N	16°57'E	80	+4.8	593	Gravelly to fine sandy till		6, 7
Blackhawk Island B.I.	43°38'N	89°47'W	289	+7.6	799	Silt loam	No ground vegetation	5, 10
Less intensively studied sites								
Mästocka 10:1	56°36'N	13°15'E	289	+6.8	1070	Sandy till	Dwarf shrub ^b	1, 8, 9
Skällarimsheden 100	66°32'N	20°11'E	280	-0.5	500	Sandy till	Dwarf shrub	
Västbyn 101	63°13'N	14°28'E	325	+2.0	455	Clayey till	Dwarf shrub ^b	8, 9
Tomta 102	59°49'N	16°33'E	63	+5.0	500	Glacial clay	Grass	8, 9
Kungs-Husby 103	59°31'N	17°16'E	30	+5.3	470	Glacial clay	Low herbs with dwarf shrubs	8, 9
Dimbo 104	59°07'N	15°44'E	70	+5.5	550	Fine sand — medium sand	Grass	8, 9
Grensholm 105	58°33'N	15°51'E	58	+6.1	525	Glacial clay	Tall herbs	8, 9
Remningstorp 106	58°28'N	13°39'E	128	+5.4	550	Glacifluvial gravel sand	Low herbs with dwarf shrubs	8, 9
Tveten 107	58°06'N	13°17'E	170	+5.4	600	Sandy till	Dwarf shrub ^b	8, 9
Sänksjön 108	58°04'N	14°08'E	245	+5.1	595	Fine—medium sand	Lichens	8, 9

^aReferences are as follows: 1, Berg et al. (1986); 2, Axelsson and Bråkenhielm (1980); 3, Holmen et al. (1976); 4, Berg and Lundmark (1985, 1987); 5, McClaugherty and Berg (1987); 6, Tamm et al. (1974); 7, Berg et al. (1987); 8, Johansson (1986); 9, Berg et al. (1991a); 10, Pastor et al. (1982).

^b*Vaccinium myrtillus*.

^cSolid fertilizer.

^dIrrigation and dissolved fertilizer.

^eSampling of litter only.

TABLE 2. Slopes for the lignin concentration increase rate (LCIR) with accumulated mass loss of decomposing, chemically similar Scots pine needle litter in natural Scots pine forests

Site No.	Intercept $\pm$ SE (mg $\cdot$ g ⁻¹)	Slope $\pm$ SE	r^2	n	p	Ref.
2	285.4 $\pm$ 34.1	2.48 $\pm$ 0.54	0.659	13	<0.001	Berg et al. 1991b
3:1	284.7 $\pm$ 12.4	1.97 $\pm$ 0.22	0.933	8	<0.001	Johansson 1986
6:51 ^a	261.8 $\pm$ 28.2	2.97 $\pm$ 0.11	0.869	104	<0.001	Berg et al. 1991b
6:51 ^b	261.4 $\pm$ 21.2	3.20 $\pm$ 0.13	0.908	65	<0.001	Berg et al. 1982, 1991b; Berg and Ekbohm 1991
8	253.1 $\pm$ 29.4	3.90 $\pm$ 0.26	0.893	28	<0.001	Berg et al. 1991b
13	263.2 $\pm$ 28.4	4.04 $\pm$ 0.23	0.903	35	<0.001	Berg et al. 1991b

NOTE: At each site several sets of incubated litter are included in the regression (cf. Appendices 3a and 3b, see footnote 2; Table 3). Significant differences in slope are indicated. All decomposition data available from sets of incubated litter at each site have been lumped together to one linear regression.

^aUnified Scots pine needle litter.

^bScots pine needle litter from the fertilized plots of site LISS plus green Scots pine needle litter.

Chemical analysis

Sites 3, 4, 6, 8, 13, and M

The combined samples were ground in a laboratory mill equipped with a screen allowing particles of less than 1 mm to pass. The amounts of water-soluble and ethanol-soluble substances were determined by sonicating the milled sample three consecutive times with fresh solvent in a sonicator bath and weighing the samples after filtration and drying. The analyses for sulfuric-acid (Klason) lignin in the needle litter samples were carried out according to Bethge et al. (1971; see also Berg et al. 1982). Nitrogen was determined by a semi-micro-Kjeldahl method using a flow-injection analysis apparatus (Bifok FIA 05, Tecator, Höganäs, Sweden) with gas diffusion and using phenol red as an indicator (Svensson and Anfält 1982). For analysis of phosphorus, sulfur, magnesium, calcium, potassium, and manganese, samples were digested for 2 days in a 2.5:1 (v/v) mixture of nitric and perchloric acid. The analyses were performed by plasma atomic-emission spectrometry ICP-AES (Instrumentation Laboratory IL P-200, Andover, Mass.).

Sites 2, 10:1, and 100-108

For the samples from these sites the following procedure was used. After a wet oxidation in H₂SO₄ total nitrogen was analyzed using a semi-micro-Kjeldahl procedure (Nihlgård 1972) and phosphorus by a molybdenum-blue method (John 1970). Potassium, calcium, and magnesium were determined by atomic adsorption spectrometry (Perkin-Elmer 603) against acid standard (Pawluk 1967). For calcium and magnesium, the analyses were made in a 0.3% LaCl₃ solution. These analyses were carried out at the same laboratory as those of the above sites and the resulting values were compatible. Lignin analysis was carried out as described above.

Site B.I.

The ground samples were extracted with dichloromethane (TAPPI 1976), followed by hot water (TAPPI 1975). Holocellulose and lignin were determined in the extract-free residue in a two-stage digestion with sulfuric acid according to the method of Effland (1977). Total nitrogen was determined using a sulfuric acid - hydrogen peroxide digestion followed by analysis of ammonium with a Technicon Auto-analyzer (TAPPI 1977). Reanalysis of site B.I. litter using the above sulfuric-acid lignin method indicated that the results from both methods are essentially identical (McClagherty and Berg 1987).

Initial chemical composition of the litter used

Initial chemical composition of the litter was described elsewhere for most of the litter (Appendix 1 for unified litter and Appendix 2 for local and experimental litter; see footnote 2) in which literature references are also given.

Data on litter mass loss and chemical changes

All basic data used for the calculations were printed in reports (see footnote 2). For sites 2, 3, 4, 6, 8, 10:1, 13, 100-108, and M, data

are found in a report by Berg et al. (1991b) and for site B.I. in a report by Aber et al. (1984). Further, the data used specifically for this paper were printed in a report by Berg et al. (1992).

Terminology and comments on lignin dynamics

We have used the word lignin to mean sulfuric-acid (Klason) lignin (nonhydrolyzable in sulfuric acid), being aware that the terminology is not entirely correct as the fraction analyzed for includes, in addition to native lignin, some humic compounds as well as some ash. The chemical similarity of lignin and humic compounds is supported by the study of Norden and Berg (1989), who found no deviations in ¹³C NMR adsorption spectra in a series of partly decomposed needle litter samples. We thus have used the term lignin here for the sake of simplicity.

To have an easily handled expression for the slope of the linear equation giving the increase in lignin concentration as a function of accumulated percent mass loss, we have used the acronym LCIR, meaning lignin concentration increase rate.

It was observed in several studies (e.g., Berg et al. 1984) that the absolute amounts of lignin normally will increase somewhat before a clear decomposition starts. For Scots pine needle litter the phenomenon was observed only in the very early stages of the decomposition process and could probably be neglected in the present case.

Conditions for selecting data

For the analysis of the variation of lignin concentration with accumulated mass loss we used only decomposition sets that had reached well into the late phase of decomposition, namely sets with an accumulated mass loss of at least 45%. Although the choice of 45% accumulated mass loss was arbitrary, we selected it to include only those data sets that had entered a stage of decomposition in which lignin concentration entered a rate-regulating stage.

In the calculations of decreasing mass-loss rate with increasing lignin concentrations we used only decomposition data from litter that was in a late decomposition phase, namely in a stage where the concentration of lignin ruled the litter mass-loss rate (Berg and Staaf 1980; Berg et al. 1987). All the litter types that were used were considered to have reached this stage by the time that they had lost at least 20% of their initial mass (regardless of the time for this), so we used only data for materials that had decomposed at least that far. The 20% mass loss selected as a limit is not connected to any time period but refers to a stage at which the litter has lost its more easily decomposable material.

Results

Overview and general comments

We first investigated differences in LCIR using several data sets with data from the following: (i) eleven sets of one litter type (unified litter) decomposing at one site; this was done

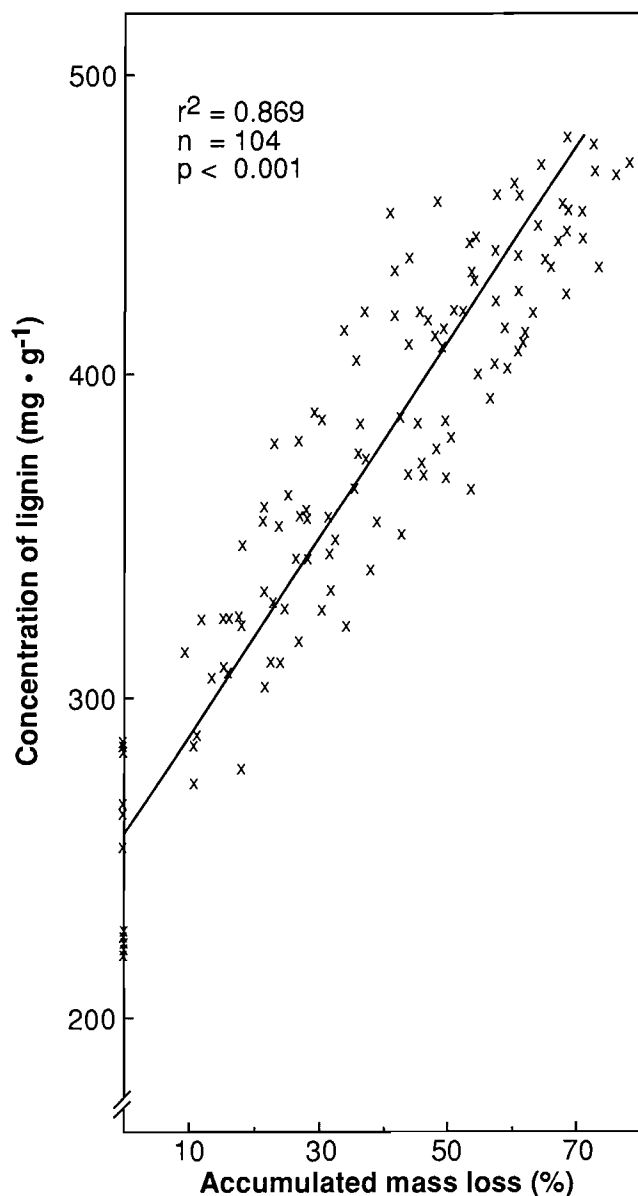


FIG. 1. The increases in lignin concentration with accumulated mass loss for 11 sets of decomposing Scots pine needle litter incubated at the site of collection (6:51) with a mor soil. The linear regression line for the slope is given.

at site 6:51 (Table 2; Appendix 3a; see footnote 2; Fig. 1); (ii) one litter type (unified litter) at five climatically different, nutrient-poor sites (2, 3:1, 6:51, 8, and 13) (Tables 2 and 3; Appendices 3a, 3b; see footnote 2; Fig. 2); (iii) local Scots pine needle litter at three plots of different nutrient status (Tables 3 and 4); (iv) both unified and experimental litter at some sites of different nutrient status including fertilized plots (sites 3, 4, and 6; Tables 3 and 7); (v) local Scots pine needle litter at several different sites (17 sites; Tables 4 and 5).

We further analyzed the change in decay rate of litter as dependent on changing lignin concentration during decomposition using the following: (i) unified litter at one site (6:51) (Table 8); (ii) unified litter at five climatically different Scots pine sites that were nutrient poor (2, 3:1, 6:51, 8, 13; Fig. 3); (iii) local litter at different sites (Table 8; Fig. 4 and 5); (iv) unified litter incubated in fertilized and manipulated Scots pine stands (sites 4 and 6; Fig. 5).

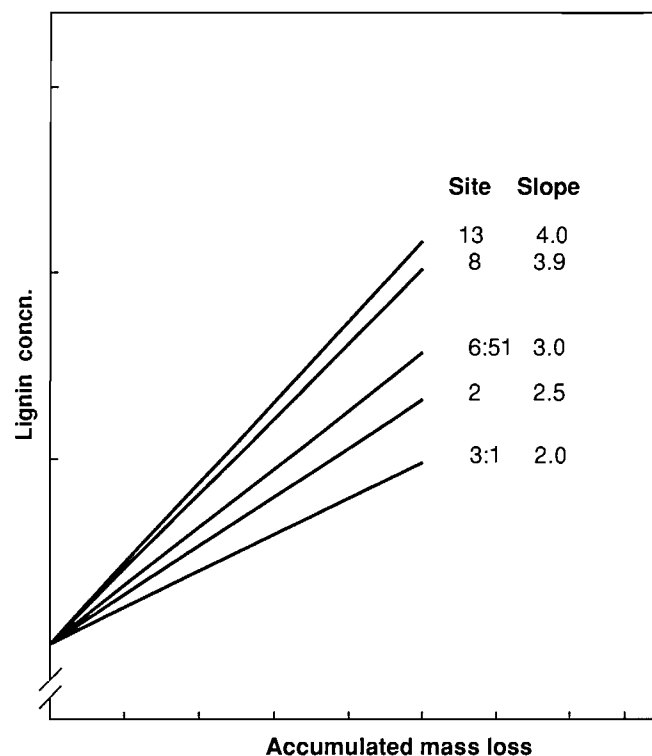


FIG. 2. The increases in lignin concentration with accumulated mass loss for different sets of decomposing unified Scots pine needle litter incubated at five climatically different sites (2, 3:1, 6:51, 8, and 13) each with a mor soil. The slopes of the regression lines for sites 2, 3:1, and 6:51 are significantly different from those of sites 8 and 13 (cf. Table 2). Further, the slopes of the line for plot 3:1 was significantly different from those of sites 6:51 and 2.

TABLE 3. Slopes for increase in lignin concentration versus accumulated mass loss (LCIR) for local litter in three nearby natural plots within one site (3, Manjärvi)

Plot No.	Intercept $\pm$ SE ($\text{mg} \cdot \text{g}^{-1}$)	Slope $\pm$ SE	r^2	n	p
1	284.7 ± 12.4	$1.97 \pm 0.22a$	0.933	8	<0.001
2	290.3 ± 13.7	$2.55 \pm 0.21b$	0.962	8	<0.001
3	270.1 ± 4.5	$2.83 \pm 0.07b$	0.996	8	<0.001

NOTE: The plots had different vegetation and soil types. Slopes followed by different letters are significantly different. Data from Johansson (1986).

Variation in the litter lignin concentration versus accumulated litter mass loss for Scots pine needle litter

Variation within one site (6:51) for unified Scots pine needle litter

When the lignin concentration increases during litter decomposition the increase versus accumulated mass loss may be described as a straight line up to relatively high mass-loss values (cf. Berg et al. 1984). A notable general phenomenon was that all needle litter types had slow and smooth increases in lignin concentrations as decomposition proceeded (Berg and Ekbohm 1991). A linear regression for all sets of unified litter incubated at this site using 104 value pairs gave a straight line with a slope of 2.970 and an r^2 value of 0.869 (Fig. 1; Table 2). When comparing the LCIR for individual litter sets we found that the slopes for chemically similar litter sets of unified litter incubated during different time periods at site

TABLE 4. The lignin concentration increase rate (LCIR) in decomposing Scots pine needle litter versus accumulated litter mass loss in locally collected litter incubated in Scots pine forests

Plot No.	Site	Max. accumulated mass loss (%)	1st-year mass loss (%)	Initial lignin concn. (mg · g ⁻¹)	Intercept ± SE (mg · g ⁻¹)	Slope ± SE	r ²	n	p
2	Harads	51.2	11.1	254.6	281.8 ± 16.7	2.57 ± 0.37	0.891	8	<0.001
100	Skällarimsheden	48.4	17.9	244.2	278.5 ± 24.6	2.74 ± 0.61	0.823	6	<0.05
3:1	Manjärvi	66.4	19.8	271.3	284.7 ± 12.4	1.97 ± 0.22	0.932	8	<0.001
3:2	Manjärvi	78.4	25.9	272.7	290.3 ± 13.7	2.55 ± 0.21	0.962	8	<0.001
3:3	Manjärvi	78.0	30.7	268.3	270.1 ± 4.5	2.83 ± 0.07	0.996	8	<0.001
101	Västbyn	83.4	36.4	261.8	263.1 ± 15.3	2.88 ± 0.22	0.968	8	<0.001
M	Malung ^a	—	—	—	277.5 ± 19.7	2.53 ± 0.11	0.907	54	<0.001
6:51	Jädraås ^b	—	—	—	261.8 ± 28.2	2.88 ± 0.11	0.869	104	<0.001
102	Tomta	79.7	36.9	254.5	278.5 ± 25.3	3.31 ± 0.37	0.919	9	<0.001
103	Kungs-Husby	69.8	38.1	225.8	227.8 ± 14.9	4.06 ± 0.25	0.982	7	<0.001
104	Dimbo	80.8	43.7	246.0	269.1 ± 24.9	3.30 ± 0.36	0.922	8	<0.001
105	Grensholm	73.1	42.0	218.8	235.8 ± 20.6	3.91 ± 0.34	0.971	6	<0.001
106	Remningstorp	79.1	35.2	254.5	258.4 ± 13.5	3.36 ± 0.19	0.979	9	<0.001
107	Tveten	73.8	36.3	347.5	330.9 ± 24.6	2.14 ± 0.41	0.901	5	<0.01
108	Sänksjön	63.9	30.0	230.5	241.2 ± 14.2	3.57 ± 0.23	0.972	9	<0.001
10:1	Mästocka	73.5	42.2	281.2	274.7 ± 16.1	3.08 ± 0.24	0.966	8	<0.001
4:23	Norrleden	51.2	17.4	284.4	290.4 ± 12.6	3.05 ± 0.22	0.953	11	<0.001

NOTE: The plots are located in a climatic transect. Maximum accumulated mass loss for the incubated litter set as well as initial lignin concentrations are given. Data from Johansson (1986) and from Berg et al. (1991b).

^aAverage slope of five incubations (cf. Table 6).

^bAverage slope of 12 incubations (cf. Table 2).

6:51 ranged between 2.30 and 3.81 (Appendix 3a; see footnote 2).

Variation among five, climatically different Scots pine sites of similar nutrient status for unified Scots pine needle litter (sites 2, 3:1, 6:51, 8, and 13)

LCIR values were compared for unified Scots pine needle litter incubated at five climatically different sites (Table 1; Fig. 2). On average sites 8 and 13 had warmer and wetter climatic conditions than did sites 6:51, 3:1, and 2, thereby promoting conditions for a higher initial decomposition rate. Under these conditions lignin concentrations increased rapidly versus accumulated mass loss with the LCIR slopes of 3.90 and 4.04, respectively. These slopes were not significantly different but were steeper than those at sites 2, 3:1, and 6:51 (colder and drier), where the slopes were 2.48, 1.97, and 2.97, respectively (Fig. 2; Table 2). This indicates a difference between the more moist and warm sites and the more cool and dry ones.

The basic equations used were all clearly significant straight lines (Appendix 3a, 3b; see footnote 2) and only unified Scots pine needle litter was used in the comparison.

Effect of climate or site on lignin-concentration increase rate for local Scots pine needle litter at several different sites

At the Manjärvi site (3) the three nearby Scots pine plots (located within a radius less than 100 m) had different hydrology and different nutrient status as indicated by soil properties and the ground vegetation (Table 1) and consequently different initial mass-loss rates for pine needle litter. The LCIR value was significantly higher than for plot 3:1 (2.55 versus 1.97; Table 3). For plot 3:3, which was the most nutrient rich and wettest and also had the highest initial mass-loss rate, the LCIR was even higher (2.83), but not significantly, than that of plot 3:2.

A data set was investigated to trace large-scale variations in LCIR values within one litter type for a wide range of climatic

situations and sites. For each site we tested the linearity of lignin concentrations versus accumulated mass loss (Table 4). In all cases except one the significance was on the level of $p < 0.001$. With the observation that natural sites with higher initial mass-loss rates (or at least a higher potential for a high mass-loss rate) also had higher LCIR values, we decided to use 1st-year mass-loss as an approximate site index for climate and nutritional conditions guiding decomposition rates.

As a first step we compared the values for LCIR (slope) and 1st-year mass-loss values by simple linear regressions, investigating Scots pine needle litter only (Table 5) and using data from sites 2, 3:1–3, 10:1, and 100–108 that were all obtained in the same investigation. The data set used (Table 4) was a set independent of those tested earlier. A clearly significant positive relation was obtained ($p < 0.05$), indicating that there was a relationship between the site properties promoting a high initial decomposition rate and the LCIR values.

Since we had found that the LCIR also varied with initial lignin concentration we made a linear regression of LCIR values versus initial lignin concentration as an independent variable. A clearly significant negative relation was obtained (Table 5), indicating that the higher the initial lignin concentration of the litter, the lower the slope of the increase. Finally, a multiple linear regression was run using both lignin and 1st-year mass loss as independent variables, which gave an r^2 value of 0.863 ($n = 14$; $p < 0.001$). Thus we may conclude that the increase rate of lignin was dependent on both site characteristics as reflected by the 1st-year mass loss and by the initial concentration of lignin. There was no correlation between initial lignin concentration and 1st-year mass loss within this transect (Table 6).

In a second step we used a larger set of data including all unified and local Scots pine needle litter as well as that of white pine incubated in natural systems. The data set also covered a wider climate range (Table 5). When LCIR values were tested versus 1st-year mass loss a significant positive

TABLE 5. Linear regressions for LCIR values versus initial lignin concentration and 1st-year mass loss (data from Table 4 and Appendix 3; see footnote 2) for a wide range of climatically different sites and leaf and needle litters

	Intercept $\pm$ SE (mg $\cdot$ g ⁻¹)	Slope $\pm$ SE	r^2	n	p
Local Scots pine needle litter from a climatic transect					
LCIR vs. 1st-year mass-loss	1.89 $\pm$ 0.52	0.036 $\pm$ 0.015	0.330	14	<0.05
LCIR vs. initial lignin concn.	6.78 $\pm$ 0.43	-0.014 $\pm$ 0.004	0.546	14	<0.01
LCIR vs. initial lignin concn. and 1st-year mass loss	5.62 $\pm$ 0.25	-0.014 $\pm$ 0.002 ^a 0.034 $\pm$ 0.006 ^b	0.863	14	<0.001
Initial lignin concn. vs. 1st-year mass loss			0.000	14	ns
All unified and local pine needle litters in natural systems					
LCIR vs. 1st-year mass loss	2.185 $\pm$ 0.658	+0.0334 $\pm$ 0.014	0.111	47	<0.05
LCIR vs. initial lignin concn.	6.820 $\pm$ 0.572	-0.0141 $\pm$ 0.003	0.387	47	<0.001
LCIR vs. initial lignin concn. and 1st-year mass loss	5.761 $\pm$ 0.544	-0.0135 $\pm$ 0.0029 ^a +0.0281 $\pm$ 0.0117 ^b	0.406	47	<0.001
Initial lignin concn. vs. 1st-year mass loss			0.009	47	ns

^aLignin.^bMass loss.

TABLE 6. Increase in lignin concentration (LCIR) with accumulated mass loss (Appendices 3a, 3c; see footnote 2) of different decomposing litter types compared at single sites

Site and litter type	Intercept $\pm$ SE (mg $\cdot$ g ⁻¹)	Slope $\pm$ SE*	r^2	n	p	Ref.
Natural systems: local litter						
Site M						
Scots pine	277.5 $\pm$ 19.70	2.55 $\pm$ 0.11a	0.907	54	<0.001	Berg and Lundmark 1985, 1987
Lodgepole pine	370.6 $\pm$ 23.61	1.24 $\pm$ 0.13b	0.617	55	<0.001	Berg and Lundmark 1985, 1987
Natural systems: transplanted litter						
Site 6:51						
Lodgepole pine						
Green needles	374.4 $\pm$ 13.25	1.71 $\pm$ 0.19	0.881	13	<0.001	Berg and Ekbohm 1991
Brown needles	386.0 $\pm$ 10.21	1.35 $\pm$ 0.13	0.902	13	<0.001	Berg and Ekbohm 1991
Site B.I.						
White pine	240.1 $\pm$ 10.70	3.12 $\pm$ 0.15a	0.977	13	<0.001	Aber et al. 1984
Eastern hemlock	222.1 $\pm$ 20.08	3.97 $\pm$ 0.32b	0.932	13	<0.001	Aber et al. 1984
Experimentally modified systems						
Site 4						
Scots pine						
Plot 4:23	255.7 $\pm$ 32.6 [†]	3.77 $\pm$ 0.27a	0.821	45	<0.001	Berg et al. 1991c
Plot 4:29	249.9 $\pm$ 23.2 [†]	4.47 $\pm$ 0.18b	0.929	51	<0.001	Berg et al. 1991c

*Slopes followed by different letters are significantly different within the same site.

[†]All incubated brown needle litter.

relation ($r^2 = 0.111$; $n = 47$; $p < 0.05$) was obtained.

The relation between LCIR values and the initial lignin concentration of the litter was highly significant and negative ($r^2 = 0.387$; $n = 47$; $p < 0.001$). When the regression was run versus both mass loss and initial lignin concentrations, the value for the correlation coefficient increased to 0.406 and the relation was still highly significant ($p < 0.001$; Table 5). To investigate for a possible correlation between 1st-year mass loss and initial lignin concentration a linear regression was run

and none was found ($r^2 = 0.009$; $n = 47$; Table 5).

Comparison of two different local needle litter types at their native sites

At site M the LCIR values were lower for lodgepole pine needle litters incubated in the lodgepole pine stand (1.24) than for those of Scots pine, incubated in the nearby Scots pine stand (2.55) (Table 6). The reason in this case is probably the higher initial lignin concentration in the local lodgepole pine

TABLE 7. The increase in lignin concentration in decomposing Scots pine needles versus accumulated mass loss (LCIR) in experimental Scots pine plantations (basic data in Appendix 4 (see footnote 2) and published by Berg et al. 1991b)

Plot No.	Intercept $\pm$ SE (mg $\cdot$ g ⁻¹)	Slope $\pm$ SE ^a	r ²	n	p
Site 4 (Norrliden)					
Plot 4:23 (control)					
Green needles	212.4 $\pm$ 20.1	5.27 $\pm$ 0.29*	0.962	15	<0.001
Brown needles	276.0 $\pm$ 27.9	2.99 $\pm$ 0.28c	0.802	30	<0.001
Green + brown needles	255.7 $\pm$ 32.6	3.77 $\pm$ 0.28a	0.821	45	<0.001
Plot 4:29 (fert.) ^b					
Green needles	211.8 $\pm$ 28.6	5.17 $\pm$ 0.12*	0.993	14	<0.001
Brown needles	261.1 $\pm$ 24.2	4.25 $\pm$ 0.22d	0.915	37	<0.001
Green + brown needles	249.9 $\pm$ 23.2	4.47 $\pm$ 0.17b	0.929	51	<0.001
Site 6 (Jädraås)					
Plot 6:15 (control)					
Brown needles	271.0 $\pm$ 17.7	3.21 $\pm$ 0.29a	0.922	12	<0.001
Plot 6:17 (irrigated)					
Brown needles	245.3 $\pm$ 12.5	3.05 $\pm$ 0.26a	0.966	7	<0.001
6:5 (fert.) ^c					
Brown needles	254.1 $\pm$ 14.2	3.57 $\pm$ 0.27a	0.963	9	<0.001
6:4 (irrig. + fert.) ^d					
Brown needles	260.3 $\pm$ 16.2	4.87 $\pm$ 0.28b	0.974	10	<0.001

^aSlopes followed by different letters are significantly different within the same site. *, indicated values are significantly different.

^bFertilized with N and P (solid fertilizer).

^cFertilized with N (solid fertilizer).

^dIrrigated and fertilized, a balanced mixture of fertilizer dissolved in water.

needles (Appendix 3c; see footnote 2), which is reflected by the intercepts being 370.6 mg $\cdot$ g⁻¹ for the lodgepole pine needles and 277.5 mg $\cdot$ g⁻¹ for the local Scots pine needles from the same site. The average slopes were significantly different and so were the intercepts.

Litter incubated under experimental conditions, viz. transplanted litter and manipulated plots

Transplanted litters: control plots

At each of the control plots 4:23, 6:51, and B.I., several transplanted litter types were incubated in addition to the local litter and the LCIR values (slopes) were compared for different litter types incubated on the same soil.

At plot 4:23 green needle litter with a high initial decomposition rate had a considerably higher LCIR value (steeper slope) than the brown needles that initially decomposed more slowly in the same plot (Table 7). With an LCIR value of 5.27 the green needles had an LCIR value almost twice that of the brown ones (2.99).

At site 6:51 we made a similar comparison and found that nutrient-enriched brown needle litter collected from a fertilized site (site LISS; Table 1) and green pine needles incubated at site 6:51 showed very similar slopes (Appendix 3a; see footnote 2). When measurement series were combined, the experimental litter gave the higher LCIR value of 3.20 (SE = 0.31; n = 65), which was not significantly different from the slope of the unified litter (2.97; SE = 0.11; n = 104) (Table 2), even if the two slopes were not far from being significantly different. Thus, we did not obtain a clear answer to whether raised nutrient levels would affect the LCIR value.

At the same site (6:51) there was a variation in LCIR values within the site when litter types varied. For brown lodgepole pine needle litter that had high initial lignin concentrations the

slopes were relatively low (Table 6), even if the slope for green needles was barely significantly steeper than that for the brown ones.

At site B.I. white pine needle litter gave a slope of 3.12, which was significantly lower than that of eastern hemlock needle litter (3.97). This shows that the data from site B.I., using different species of needle litter, fit to the results shown in Fig. 2 and Table 5. The climate (temperature and precipitation) of site B.I. is intermediate to those of sites 6:51 and site 8 and the slopes (see above) thus fit well with the pattern indicated by climate alone. Further, the initial lignin concentrations of the two litter types (hemlock 206 and white pine 225 mg $\cdot$ g⁻¹) also fit the observation that LCIR is influenced by initial lignin concentration.

Variation between control plots and fertilized plots

We compared increase rates in lignin concentration (LCIR values) for Scots pine needle litter in some fertilization experiments. Chemically identical needle litter was incubated at two different sites (4 and 6) where heavy dosages of nitrogen and phosphorus fertilizer had been applied. It was clear that the LCIR in different needle litter types was significantly higher in the fertilized plots than in the control plots. Thus, for brown needles at site 4 the increase rates were 4.25 and 2.99, respectively, and significantly different at a fertilized plot (4:29) and at a control plot (4:23), respectively (Table 7). Within the same plot, green needle litter gave higher slopes than the brown needle litter, i.e., in the control plot with 5.27 compared with 2.99, and within the fertilized plot with 5.17 versus 4.25. In each case the difference was significant. When combining all litter types in the control plot, the slope of the control plot litter (3.77) was still significantly lower than that of the litter from the fertilized one (4.47).

TABLE 8. A comparison of the rate-regulating effect of lignin in some sets of chemically different pine needle litter incubated at sites 6:51, B.I., and M (basic data published by Berg et al. 1991b)

Litter type	Slope $\pm$ SE	Intercept $\pm$ SE ($\text{mg} \cdot \text{g}^{-1}$)	r^2	n
Site 6 Scots pine				
Control plot 6:51				
Unified ^a	-0.078 ± 0.016	54.86 ± 3.46	0.478	29
Experimental	-0.085 ± 0.016	58.634 ± 3.01	0.633	18
Control plot 6:15	-0.095 ± 0.019	55.29 ± 2.80	0.652	16
Irrig. + fert. plot 6:4	-0.116 ± 0.025	91.71 ± 3.17	0.849	9
Site M				
Scots pine	-0.190 ± 0.027	103.95 ± 4.50	0.801	14
Lodgepole pine	-0.189 ± 0.071	106.59 ± 9.29	0.371	14

^aAt this site the unified litter also was the local litter.

At site 6 the LCIR values were 3.57 and 3.21 for unified Scots pine needle litter in the fertilized plot (6:5) and the control plot (6:15), respectively (Table 7). The litter incubated in the control plot was initially identical to that in the fertilized one. Irrigation only (plot 6:17) did not increase the slope whereas irrigation plus fertilization (plot 6:4) gave a steeper slope (4.87) that was significantly different from the LCIR values for other treatments at this site. In all those cases unified litter was compared.

Effect of lignin concentrations on mass-loss rate: late stages of decomposition

One site – one litter species (unified litter; site 6:51)

To focus on later decomposition stages we considered only data sets with > 20% accumulated mass loss, when lignin concentrations had increased enough to retard the litter mass-loss rate (McClaugherty and Berg 1987; Berg and Staaf 1980). We examined the effect of lignin concentrations at the beginning of a 1-year period on the mass-loss rates of the litter during that 1-year period.

For one site (6:51) we tested the effect of lignin concentration on mass-loss rates in later stages of decomposition using unified Scots pine needle litter (Table 8; Fig. 3). The relation was highly significant ($r^2 = 0.478$; $n = 29$; $p < 0.001$). The annual mass loss thus decreased from 30% per year at a lignin concentration of $320 \text{ mg} \cdot \text{g}^{-1}$ to 20% per year at a lignin concentration of $440 \text{ mg} \cdot \text{g}^{-1}$. For this site there are earlier reports on the decrease in mass-loss rate (Berg and Ågren 1984; McClaugherty and Berg 1987) related to increasing lignin concentration.

Comparison of the decomposition rates for two different litter types incubated at site 6:51

At site 6:51 (a mor site) data from two different types of incubated Scots pine needle litter were compared (Table 8); the unified litter and some sets of experimental Scots pine needle litter from fertilized trees. The two sets had initially different chemical composition in terms of nutrients, with the experimental ones having about 2–3 times higher concentrations of nitrogen, phosphorus, and sulfur as the unified litter. When correlating annual mass loss versus the lignin concentration of the litter at the start of each 1-year period, the experimental litter gave a steeper slope (-0.085) than the unified litter (-0.078), but the slopes were not significantly different. This indicates that for a given species and site the initial nutrient composition of the litter may have a limited influence on lignin regulation of mass-loss rate.

Five climatically different sites (unified litter; sites 2, 3:1, 6:51, 8, and 13)

We compared the effect of lignin concentration on litter mass-loss rates for five sites that were climatically different but had similar nutrient status (2, 3:1, 6:51, 8, and 13). For the five sites investigated, the slopes were partly different and formed a pattern. The steepest slopes were those estimated for sites 13 and 8, both of which had the highest precipitations and highest mean annual temperatures (Table 1) and consequently the highest initial decomposition rate. The slopes (-0.250 and -0.211) were not significantly different, but both were significantly steeper than the slopes from the other three sites, indicating that the lignin concentration had a clearly stronger effect on mass-loss rates at these two sites compared with the other ones.

Litter types incubated on sites 2 and 3:1 had very similar slopes, whereas that at 6:51 was clearly higher and significantly different from the other ones. Although sites 3:1 and 2 are cooler, they have a higher mean annual precipitation than site 6:51 (Table 1), but the initial decomposition rates are lower than at site 6:51. The effect of lignin concentration was significantly stronger for site 6:51 than for site 2 (Fig. 3), and we may distinguish two main groups of sites and an intermediate one. In fact, the influence on litter mass-loss rates was so low at the two cooler sites and the regression lines were so shallow that they were not significant. Thus, over a broad range of climates, decomposition rates were more sensitive to increases in lignin concentration at warmer, more mesic sites (e.g., sites 8 and 13). The reason for a stronger effect of lignin may be related to the faster increase in lignin concentration observed (cf. Fig. 2). Composition of the microbial population could depend on climate and we may thus speculate that this ruled the observed phenomenon. The litter that initially were being degraded more quickly could thus have a microflora that preferentially decomposed the celluloses, resulting in a relatively lower proportion of the lignin being degraded. With a higher concentration of lignin, the remaining litter would thus be more recalcitrant. The cooler and drier conditions may limit the activity of the cellulose-decomposing organisms and allow the more slowly growing lignin decomposers to develop, thus allowing a higher proportion of the lignin to be degraded. This would then give litter at the warm and wet sites a higher proportion of lignin and a lower proportion of celluloses, and the opposite for litter at the drier and colder sites. This view is in part supported by an independent study on lignin decomposition rates in a climatic transect along Sweden. We actually observed the highest rates close to the Arctic Circle and clearly

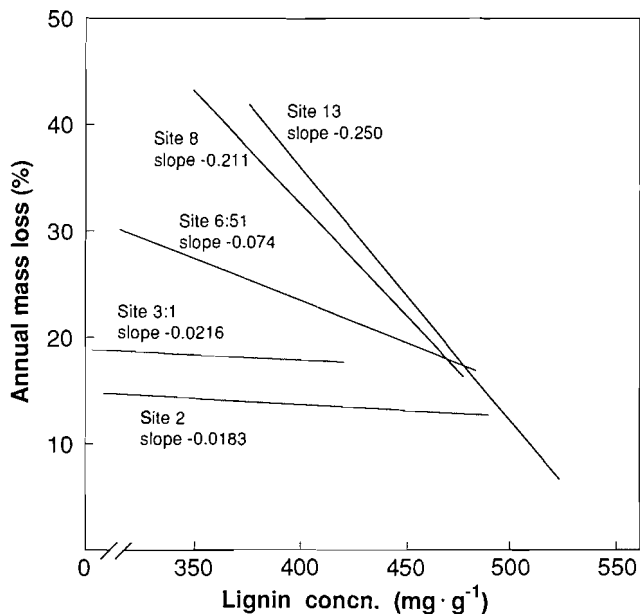


FIG. 3. Linear relations for annual mass loss as dependent on lignin concentration at the start of each 1-year period at five climatically different sites (2, 3:1, 6:51, 8, and 13). The slopes for the regression lines are all significantly different.

lower rates in the south of Sweden where the climate otherwise could be considered more favourable to decomposition i.e., wetter and warmer (B. Berg and M.-B. Johansson, unpublished data).

The litter types used in the comparison were local Scots pine and unified litter (Fig. 3) that had initially rather similar concentrations of nitrogen and phosphorus as well as lignin (approximately 2.5–4.2, 0.20–0.34, and 223–288 $\text{mg} \cdot \text{g}^{-1}$, respectively). The interval of lignin concentrations used in the linear regressions was similar among the sites (site 2, 343–475 $\text{mg} \cdot \text{g}^{-1}$; site 3:1, 314.0–400.6 $\text{mg} \cdot \text{g}^{-1}$; site 6:51, 315–442 $\text{mg} \cdot \text{g}^{-1}$; site 8, 302–460 $\text{mg} \cdot \text{g}^{-1}$; and site 13, 380–520 $\text{mg} \cdot \text{g}^{-1}$). A linear regression was also run to compare the slopes at site 8 and 6:51 using an interval for lignin concentration that was exactly the same for both sites. No change in slope was seen, although the correlation coefficients were somewhat lower.

Comparison of the decomposition rates for two different litter types incubated at their individual stands (site M)

At site M (a mor site) field incubations were made using local Scots pine and lodgepole pine needle litter, and in both cases the mass loss was followed to about 65–75%. For decomposition in the 2nd, 3rd, and 4th years we tested the influence of lignin concentration on litter mass-loss rate for each species separately and found two significant linear relations (Fig. 4). The relation for Scots pine needle litter was highly significant ($r^2 = 0.794$; $n = 15$; $p < 0.001$), whereas that for lodgepole pine needle litter was more diffuse even if significant ($r^2 = 0.289$; $n = 16$; $p < 0.05$) (Fig. 4). The two straight-line relations were almost parallel and neither their slopes nor their intercepts were significantly different (Table 8).

Unified litter incubated in an experimental Scots pine stand (irrigated and fertilized stands; site 6)

In a manipulated forest at site 6, two stands were compared at the same site, namely a control stand (6:15) and an irrigated plus fertilized (IF) stand (6:4).

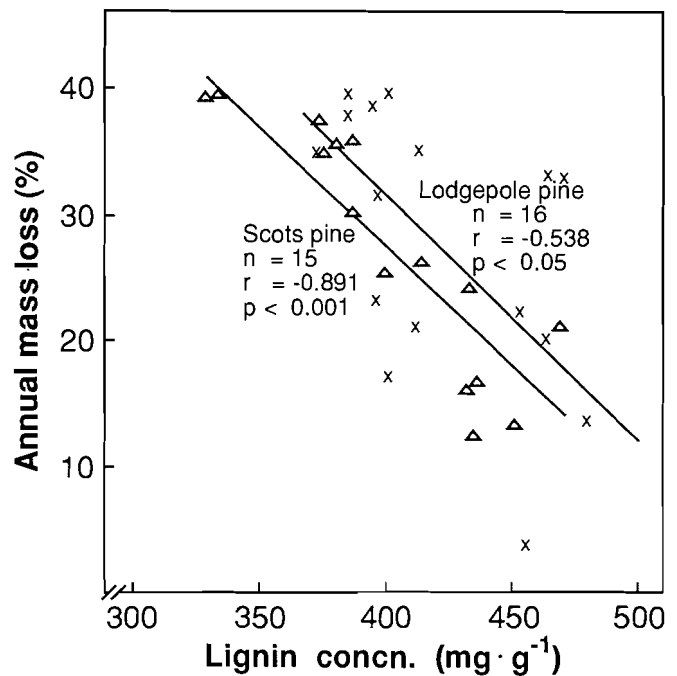


FIG. 4. Linear relations between annual mass loss from decomposing lodgepole pine (X) and Scots pine (Δ) needle litter and the concentration of lignin at the start of each 1-year period. The regression lines are not significantly different (from Berg and Lundmark 1985, 1987).

In later decomposition stages (>20% accumulated mass loss), decomposition rates decreased for litter in both the control stand and in the plot with a combined irrigation and fertilization treatment (IF plot; basic data from Berg et al. 1991c). The effect of lignin concentration was significantly stronger in the IF plot (Fig. 5), as the slope of the regression line between lignin concentration and annual mass loss was considerably higher (slope = -0.156 ; $r^2 = 0.849$; $n = 9$; $p < 0.001$) (Table 8) than that of the litter in the control plot (slope = -0.095 ; $r^2 = 0.652$; $n = 16$; $p < 0.001$).

The plot with combined irrigation and fertilization had conditions that raised the initial mass-loss rate for litter as compared to those of the control plot. It thus appears that in this manipulated plot we obtained results similar to those observed in a geographically long climatic transect.

Discussion

Different increase rates in lignin concentration

The fact that lignin concentration in decomposing litter increases with different rates may be explained by an interaction of factors limiting the activity of the microbial decomposers and possibly a difference between microbial communities. A possible interpretation is that under warmer and wetter conditions climate is less limiting, if limiting at all, for the microbial community. The fungi and bacteria that decompose the relatively easily degraded cellulose and hemicellulose could invade the litter and degrade them at a higher rate. Lignin is less energy rich and thus not primarily attacked and degraded more slowly. Consequently climatic conditions that favour a high degradation rate of celluloses would not affect the lignin degradation to a comparatively high degree. Thus there would be a proportionally higher decomposition rate of the cellulose fractions, and the concentration of lignin would increase more quickly. Under soil climatic conditions that are less favourable,

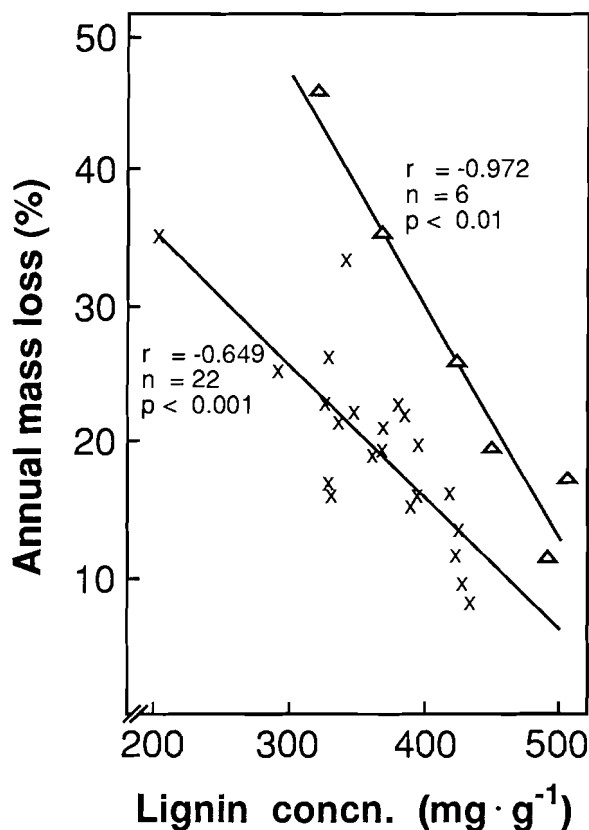


FIG. 5. Annual mass loss of litter plotted versus lignin concentration at the start of each 1-year period for experimental plots at site 6. Litter in control plot (x) and irrigated plus fertilized plot (Δ). Data from Berg et al. (1991c).

viz. lower temperature and lower precipitation, the difference in degradation rates between the celluloses on one hand and lignin on the other would be less, and consequently the increase in lignin concentration would be relatively slower versus the accumulated mass loss.

This interpretation may also be used to explain the relatively higher increase rates of lignin in litter that has higher nutrient levels (e.g., green needle litter) and the higher increase rates in lignin concentrations in litter in fertilized forest stands (Tables 2 and 7). Raised nutrient levels tend to enhance the decomposition rates of chemical components in litter, such as cellulose, hemicelluloses, and soluble substances (cf. Berg and Staaf 1980), and the effect, in this case, would be a higher increase rate in lignin concentration.

The present paper presents observations that were made in ecosystems in which pines are the dominating species. In addition Berg and Tamm (1991) reported a similar observation in a Norway spruce forest. Even so, we may not conclude that this type of effect is general. The pattern of lignin dynamics described here may not hold in systems with a high activity of soil fauna. Also, the soil microbial community could behave differently in other systems. For example, in soils that are dominated by microbial populations with the ability to utilize the energy in lignin, e.g., some white-rot organisms, the pattern may be different.

However, we may conclude that both site characteristics and lignin concentration in the litter were important factors in

determining the increase rate in lignin concentration for a wide range of sites and litters and that lignin concentration may be the dominating factor in that relation.

Differences in the effect of lignin on mass-loss rates

The concentration of lignin had increased more quickly (relative to accumulated mass loss) at the warmer and wetter sites (Fig. 2), thus having an effect on the litter quality that clearly could influence subsequent mass-loss rates. This possibly would be part of the observed effect and it appears reasonable to conclude that the influence of lignin on mass-loss rate was caused both by litter properties and by climatic factors at each site. In an earlier paper Berg and Ekbohm (1991) observed at a given site (6:51), and thus a given climatic situation, that the faster the decomposition in the earlier stages, the slower the decomposition in the later phase. This kind of empirical finding supports the discussion above that factors (in this case substrate quality factors) that promote high initial mass-loss rate (including the decomposition of cellulose) leave higher lignin concentrations, and the whole insoluble fraction becomes more resistant. The strong effect on mass-loss rate in warmer and wetter climatic situations could in part be influenced by the interaction of two counteracting influencing factors. With climate factors more optimal, the effect of lignin could be seen more clearly. As lignin decomposition is a slow process, a consequence is that the decomposition rates of whole litter in late stages of decomposition (e.g., at lignin concentrations $> 450 \text{ mg} \cdot \text{g}^{-1}$) are regulated so strongly by lignin that the climatic influence would be much less pronounced than in early stages (cf. Berg and Ågren 1984; McClaugherty and Berg 1987).

In a comparative study, lignin concentration could explain approximately 80% of the mass-loss rate for Scots pine needles in late stages ($r^2 = 0.801$), whereas the corresponding figure for lodgepole pine needles was 37% ($r^2 = 0.371$; Fig. 4; Berg and Lundmark 1987). It thus appears that for the lodgepole pine needles, some other factor(s) may be more important in controlling the rate. Whereas for Scots pine needles the concentration of lignin increased relatively quickly from approximately $200\text{--}250 \text{ mg} \cdot \text{g}^{-1}$ initially up to approximately $500 \text{ mg} \cdot \text{g}^{-1}$ as a final value (reached asymptotically, cf. Berg et al. 1984; Berg and Ekbohm 1991), the lodgepole pine needles started with an initial value of approximately $380\text{--}390 \text{ mg} \cdot \text{g}^{-1}$ to reach about the same maximum value. The more narrow range for lodgepole pine needles may explain the greater scatter (and lower r^2 value) for this litter type.

The annual mass-loss rates for unified Scots pine needle litter measured at the control and IF plots were plotted versus concentrations of lignin at the beginning of each 1-year period (Fig. 5). In both cases highly significant linear relations were obtained with $r = -0.649$, $n = 22$, and $p < 0.001$ for the control plot and $r = -0.972$, $n = 6$, and $p < 0.01$ for the IF plot. Although the litter mass-loss values for the IF plot were clearly above those of the control plot at the same lignin concentration (Fig. 5), the regression line for mass-loss rates of the IF plot had a considerably steeper slope and a higher intercept than that of the control plot litter (Fig. 5). Similar to the corresponding lines in Fig. 3, the two regression lines converged, and one might expect that at some point above a concentration of $500 \text{ mg} \cdot \text{g}^{-1}$ of lignin they should either cross each other or approach a common maximum value (cf. McClaugherty and Berg 1987). Furthermore they seem to con-

verge at a mass-loss rate of about 10% per year. The steeper slope means that although the litter in the IF plot had a higher initial mass-loss rate, mass-loss rates declined more rapidly at higher lignin concentrations than they did in litter on the control plot. The lines may converge at a lignin concentration of 50% and a rate of 10% per year.

An observation that may be compared with the present one was made by Söderström et al. (1983). When measuring soil respiration rates in a set of nitrogen-fertilized plots they found a highly significant, negative effect of nitrogen amendments on microbial respiration from humus as well as on live bacterial biomass (direct counts). The fixation of ammonia to organic material and the consecutive chemical reactions have been suggested to produce more recalcitrant compounds (Berg and Ekbohm 1991). A higher initial mass-loss rate and consequently also mineralization rate may thus have that kind of effect (for a review see Nömmik and Vahtras 1982). Products of lignin degradation may react with ammonia or amino acids to form recalcitrant complexes (Bremner and Shaw 1957). The results of laboratory experiments indicate that the concentration of ammonium or ammonia could be rate-limiting for this kind of reaction to proceed (Axelsson and Berg 1988).

A further possible contributing factor is the observation by Keyser et al. (1978) and Kirk et al. (1978) who found that amino acids and ammonium ions repressed the formation of lignolytic enzymes in one fungal species. There now appear to be several species that have this kind of repression (P. Ander, personal communication). Although substrate quality, and lignin in particular, plays an important role in regulating litter decomposition rates, the pattern of changes in lignin concentration during decomposition can be significantly influenced by site factors such as climate and nutrient availability. The mechanisms underlying these observations and their applicability in other ecosystems have yet to be determined.

Provided that the finding of ligninase repression is correct and reflects a more general phenomenon, one could expect that higher amounts of mineralized and low-molecular nitrogen would appear per time unit in connection with a higher turnover rate. This nitrogen may react with lignin remains, form recalcitrant compounds, and thus decrease the lignin degradation rate and consequently also the litter mass-loss rate.

It is thus reasonable to assume that either one or both of these mechanisms may contribute to decreasing the decomposition rate of lignin. Such a mechanism may suggest that at sites with climatic and nutritional factors allowing high initial rates, we may expect that an accumulation of partly decomposed litter may take place. Possibly such an accumulation would go at a higher rate there than at climatically more unfavourable sites.

The observations made in this paper may in part be disturbed by the ingrown fungal biomass, as part of the mycelium, e.g., chitin, may disturb the lignin analysis. On the other hand, in Scots pine needles at different nutrient levels, Berg et al. (1987) observed that the measurable amounts of total mycelium were relatively small, less than 1.5% of the litter mass, also in late decomposition stages.

Integration of the two phenomena described here, namely climatic and site quality influences on LCIR and the effect of lignin concentrations on mass-loss rates, goes beyond the scope of the present paper. Such an integration may prove helpful in understanding the dynamics of litter in later stages of decay as it approaches humus.

Acknowledgement

We are grateful for the constructive comments given by two anonymous referees.

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